

expression is responsible for the *cre1 ahk3* phenotype, because loss of AHP6 function in *ahp6-1 cre1 ahk3* was able to suppress the ectopic protoxylem (91%;  $n = 45$ ) (Fig. 1B). In both *wol* and *cre1 ahk2 ahk3*, the AHP6 expression pattern expands throughout the vascular bundle (Fig. 4A) (12). The expanded expression pattern in *wol* is already evident by the early torpedo stage of embryogenesis when it occupies one broad domain within the embryonic root as opposed to two narrow strands in wild-type (Fig. 3F and fig. S8C). This indicates that cytokinin signaling specifies the spatial domain of AHP6 expression upstream of protoxylem differentiation, which occurs after embryogenesis. Next, we examined the effect of exogenous cytokinins on AHP6 expression. We observed down-regulation of the AHP6 transcript after a 6-hour treatment with cytokinins (Fig. 4B). Likewise, the level of fluorescence in the *AHP6prom::GFP* line was reduced by cytokinins, and the reduction occurred at lower levels of cytokinin in *ahp6-1* than in wild-type roots. (Fig. 4C and fig. S9). In the absence of applied cytokinin, the levels of AHP6 transcript in *ahp6-1* were slightly lower than in the wild type (12).

We report a regulatory circuit between cytokinin signaling and its newly identified inhibitor, AHP6, which specifies the meristematic versus differentiated nature of procambial cell files (Fig. 4D). In this sense, our results are consistent with requirement of cytokinins for transdifferentiation of xylem observed in *Zinnia* mesophyll cell culture (5, 19). AHP6 can be considered the founding member of a new “pseudo” subclass of HPT proteins within the wider group present in prokaryotes and eukaryotes.

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#### Supporting Online Material

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Materials and Methods

SOM Text

Figs. S1 to S9

References

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## Fishing, Trophic Cascades, and the Process of Grazing on Coral Reefs

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Since the mass mortality of the urchin *Diadema antillarum* in 1983, parrotfishes have become the dominant grazer on Caribbean reefs. The grazing capacity of these fishes could be impaired if marine reserves achieve their long-term goal of restoring large consumers, several of which prey on parrotfishes. Here we compare the negative impacts of enhanced predation with the positive impacts of reduced fishing mortality on parrotfishes inside reserves. Because large-bodied parrotfishes escape the risk of predation from a large piscivore (the Nassau grouper), the predation effect reduced grazing by only 4 to 8%. This impact was overwhelmed by the increase in density of large parrotfishes, resulting in a net doubling of grazing. Increased grazing caused a fourfold reduction in the cover of macroalgae, which, because they are the principal competitors of corals, highlights the potential importance of reserves for coral reef resilience.

Caribbean reefs were acutely disturbed in 1983 when the herbivorous urchin *Diadema antillarum* experienced mass disease-induced mortality (1). In the absence of *Diadema*, parrotfishes (Scaridae) have become the dominant grazer on most Caribbean reefs (2). Grazing performs several critical functions in this ecosystem, including the conversion of primary production to fish-based trophic pathways (3), the provision of suitable settlement substrata for new corals (4), and the mediation of competition between corals and macroalgae (5). Parrotfishes are exploited in many parts of the region, and several studies

have reported increases in their density when fishing intensity was reduced inside reserves (6, 7). However, although reserves may benefit parrotfish populations in the short term, these impacts may be reversed on longer time scales. Most reserves aim to restore the biomass of large piscivores (8) such as the Nassau grouper (*Epinephelus striatus*), but this might eventually cause cascading top-down limitation on the biomass of their prey (9, 10), which includes parrotfishes (11, 12). Therefore, with the continued scarcity of *Diadema* (13), the realization of a successful reserve may impair levels of grazing and its associated ecosystem functions.

Few reserves are either large, old, or effective enough to have had a significant impact on large predators (6, 14). An exception is the Exuma Cays Land and Sea Park (ECLSP), which lies near the center of the Bahamas archipelago. The ECLSP is large (456 km<sup>2</sup>) and was established in 1959. A ban on fishing has been enforced there since 1986, and the current biomass of *E. striatus* is seven times greater in the ECLSP than that observed in three other regions of the archipelago (15). The ECLSP is, therefore, one of the few places in the Caribbean where the long-term impacts of reserves can be investigated (16). We sampled four island systems at hierarchical scales and contrasted the results in and around the reserve with those found at equivalent spatial scales in systems that lacked reserves. Specifically, fish communities of *Montastraea* reefs were sampled at scales of sites (hundreds of

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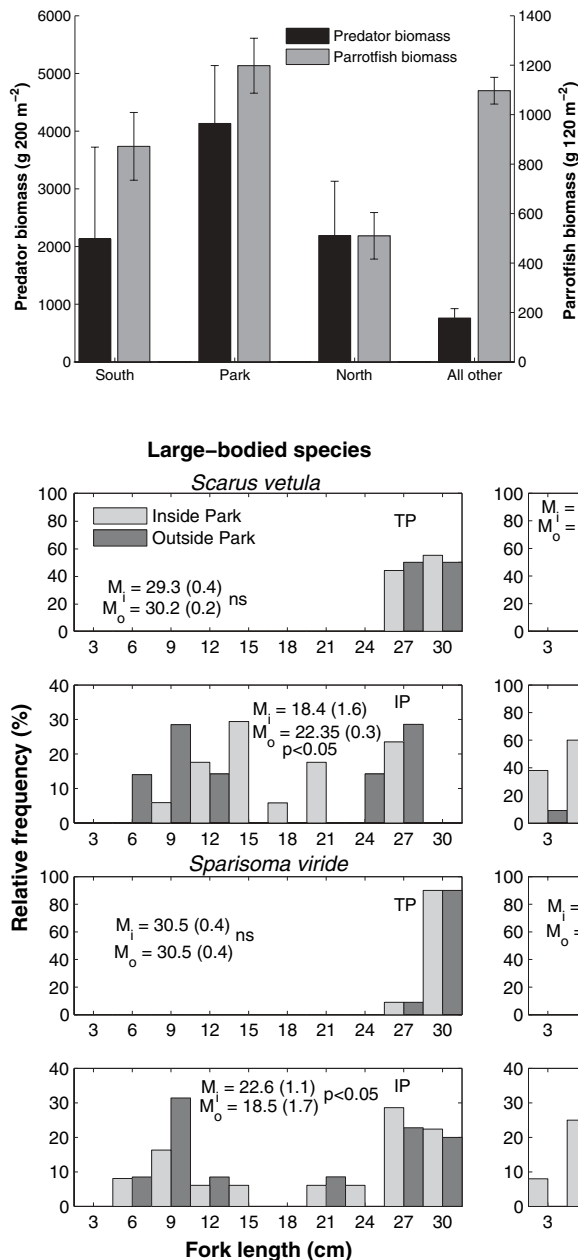
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meters,  $n = 3$  to 4), reefs (or reserve) (tens of kilometers,  $n = 3$ ), and island systems (hundreds of kilometers,  $n = 4$ ). The reserve is located between two nonreserve reefs, to the north and to the south of the reserve, in the Exuma Cays island system. To examine the influence of reserves on grazing, we created and tested a model of parrotfish grazing intensity that was sensitive to species, size, and life phase (16).

The overall biomass of all parrotfish predators within the reserve was approximately double that found in nonreserve areas within the same reef tract and was more than five times greater than that in other regions of the archipelago (Fig. 1). *E. striatus* accounted for 45% of this predator biomass, with the remainder being composed of other large groupers, including *Mycteroperca tigris* (27%) and a combination of Sphraenidae, Muraenidae, and large Lutjanidae (28%).

At the scale of reefs within an island system (tens of kilometers), the community structure of parrotfishes showed significant variation only between the reserve and its immediate nonreserve reefs (analysis of similarities,  $R = 0.29$ ,  $P < 0.05$ ). Several parrotfish species exhibited significant differences in size across reserve boundaries (Fig. 2). Individuals of the smaller bodied scarid species, whose maximum length rarely exceeds 23 cm (*Scarus iserti* and *Sparisoma aurofrenatum*), were smaller inside the reserve (Fig. 2), but their densities were indistinguishable from those elsewhere [analysis of variance (ANOVA),  $P > 0.05$ ]. In contrast, scarids that reached consistently large adult sizes, such as the terminal-phase (TP) males of *Sc. vetula* and *Sp. viride*, exhibited no difference in their size across the reserve boundary (Fig. 2), but their mean density was nearly doubled inside the reserve. Parrotfishes that occupied a wide range of size categories (6 to 32 cm) were either larger in the reserve [*Sp. viride* intermediate phase (IP)] or larger outside the reserve (*Sc. vetula* IP). Mean parrotfish sizes outside the reserve did not differ from those found elsewhere in the archipelago ( $P > 0.05$ ).

Large-bodied parrotfishes appear to escape predation by the dominant piscivore, *E. striatus* (Fig. 3). The distribution of mouth sizes in the grouper population is such that few groupers (typically  $<0.5$  individuals per 1000  $m^2$ ) are large enough to swallow TP parrotfish of the larger bodied species *Sc. vetula* and *Sp. viride* (Fig. 3), and such large groupers were observed only in the reserve. In contrast, between 60 and 90% of the *E. striatus* in the reserve are able to consume adults of the smallest bodied parrotfish, *Sc. iserti*, and 30 to 60% of groupers are able to swallow the medium-sized scarid, *Sp. aurofrenatum*. Adults of both parrotfish species were significantly smaller inside the reserve (Fig. 2). An increase in natural predator-caused mortality within the reserve would be expected to reduce their average longevity and therefore length (17) and grazing capacity (18).



**Fig. 1.** Patterns of parrotfish biomass and their predators ( $\pm$ SE) within the Exuma Cays and for all other surveyed areas combined. "Park" denotes the ECLSP.

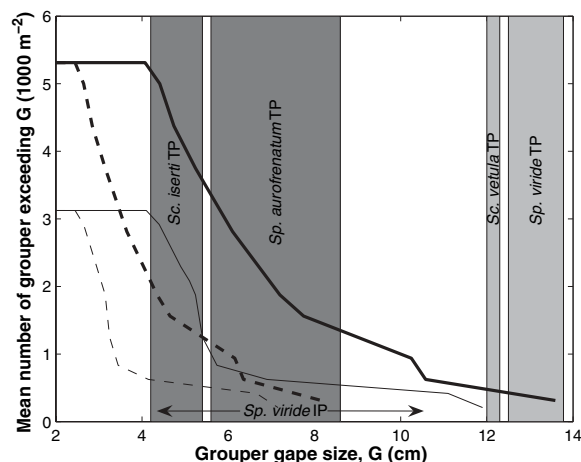
**Fig. 2.** Relative size frequency distributions of four parrotfish species in two life phases (TP and IP). Data were pooled for the *Montastraea* reef habitat inside and outside the ECLSP. Also shown are the mean ( $\pm$ SE) length of species inside ( $M_i$ ) and outside ( $M_o$ ) the reserve and the probability of a  $t$  test finding no significant difference between sites. "Fork length" is measured from the snout to the fork of the tail.

The optimal size of prey for many piscivorous fishes is 0.6 times that of the predator's jaw width (19); chasing larger prey may be uneconomic because of the greater evasive potential of larger individuals (20). Therefore, predator capacity was also plotted for the assumption that prey choice was restricted to the most preferred individuals [those with body height not exceeding 60% of grouper jaw width (Fig. 3)]. Under this scenario, a grouper's capacity to consume the smaller bodied species remains greater in the reserve, whereas the likelihood of consuming TP *Sc. vetula* or *Sp. viride* is even less, emphasizing

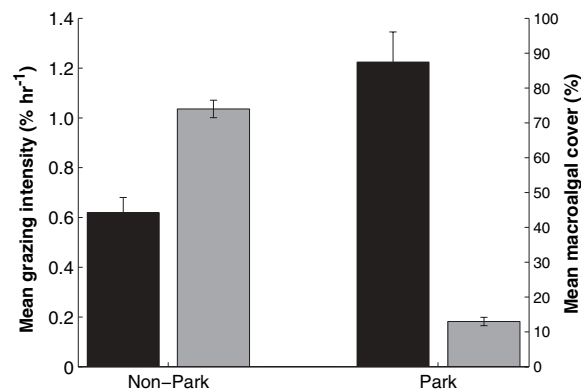
the potential for a size escape from predation. However, foraging by *E. striatus* is primarily nocturnal and crepuscular (12, 21) and is therefore coincident with the nocturnal resting of parrotfishes (22), often in vulnerable locations on the reef. Prey may be much less likely to escape under these circumstances, thereby increasing the probability that groupers will prey on scarids with dimensions approaching the upper limits of mouth size (though it appears that *Sc. vetula* and *Sp. viride* are able to avoid this increased vulnerability).

Our data suggest that the fishing mortality of large-bodied parrotfish is considerable in

**Fig. 3.** Consumptive capacity of Nassau grouper populations inside (bold lines) and outside (light lines) the ECLSP. Solid lines assume that prey consumption is constrained by the full width of grouper mouthparts, whereas dotted lines represent an optimal prey size equivalent to 60% of the full gape. Dorsoventral heights of parrotfish (prey) species were plotted for the observed range of scarid size in the Exuma Cays. Dark and light shading denote the size ranges of small- and large-bodied parrotfishes, respectively.



**Fig. 4.** Mean grazing intensity of parrotfishes (black bars) and macroalgal cover (gray bars) ( $\pm$ SE) inside and outside the ECLSP. Reserve impacts are significant ( $P < 0.01$ ) for each variable.



fished areas of the Exuma Cays. Of the large commercial fishing vessels registered as using fish traps in the Bahamas, 40% (14) have sufficient size ( $>10$  m) and proximity (Nassau to Exuma Cays) to fish around the reserve (23). An additional 30 traps are deployed locally to the south of the reserve. Large-bodied parrotfish are highly susceptible to fish traps (6), which may be left unattended during periods of high winds and cause considerable, though not quantified, mortality of parrotfishes. Studies in Barbados found traps to be disproportionately selective for *Scarus vetula* (6), and the biomass of this species was almost seven times greater inside the reserve. Overall, the total biomass of parrotfishes was significantly greater inside the reserve (Fig. 1,  $P < 0.001$ ). We conclude, therefore, that larger parrotfishes have benefited numerically from a reduction in fishing pressure within the ECLSP.

The results of nested analyses allow us to infer that the reserve has significant effects on predator biomass and on the community structure, size distribution, and grazing intensity of parrotfishes. Even if we assume that only 2 of the 12 inter-reef comparisons exhibit significant differences, the probability that both involve the reserve is  $\sim 1\%$ . Fully functioning marine reserves in the Caribbean appear to have a negative impact on the size distribution of smaller bodied parrotfish through

increased predation, but a positive impact on larger bodied species because of the release from fishing pressure. With the continued paucity of *Diadema* (13) and the nonlinear positive relationship between fish length and grazing intensity (18), any impact on larger bodied fishes will have a disproportionately large impact on grazing. In this system, the net impact of reserve implementation was a doubling of total scarid grazing (Fig. 4), and this reef-level effect was observed only across reserve boundaries (nested generalized linear model ANOVA,  $P < 0.05$ ).

The cover of living coral on Bahamian reefs was severely reduced by bleaching during the exceptionally high sea temperatures of the 1998 El Niño–Southern Oscillation event (13). Given projected climate change, the resilience, or ability of reefs to recover from such disturbances, is a key societal concern (24). Recovery requires the successful recruitment and survival of new corals, but both processes are inhibited by macroalgae (5, 25). Our data reveal a strong negative relation between fish grazing intensity and macroalgal cover in the Exuma Cays; the cover of macroalgae was reduced fourfold inside the reserve (Fig. 4), whereas there were no reef-scale fluctuations in cover in systems with no reserve ( $P > 0.40$ ). Although the biomass of herbivorous fishes has been negatively correlated with macroalgal

cover on a Caribbean-wide scale (26), the direct small-scale impacts of a reserve were previously undocumented. Although reductions in macroalgal cover inside reserves may enhance the recruitment and survival of corals, elevated parrotfish grazing may have complex impacts on reefs. Scarid grazing is an important source of bioerosion, and although only 4% of their bites are taken from adult corals (18), the role of parrotfishes as predators of juvenile corals is yet to be evaluated.

The “benefits” accrued from a reserve will largely depend on the intensity of fishing outside its boundaries. If Caribbean parrotfishes were not affected by exploitation at all, then a reserve would cause only negative impacts on parrotfishes because of enhanced predation. Rescaling the size of each parrotfish using the mean size discrepancies reported in Fig. 2, we calculate that the total grazing intensity would drop by 4 to 8% of its current value in several island systems (San Salvador, the Turks and Caicos Islands, and Andros) where parrotfish exploitation is relatively light (fish traps are used on  $<1\%$  of fishing trips). A predation-based reduction in grazing of 4 to 8% would be fully compensated for if the reserve enabled parrotfish densities to increase by a mean level of 9% (approximately one individual of each life phase of each species in 1200  $m^2$ ). To place this reserve impact in perspective, it represents just one-sixth that observed in the Exuma Cays, which by Caribbean standards is a relatively lightly fished system. For example, scarid grazing intensity in fished regions of the Exuma Cays was at least five times greater than in exploited areas of Jamaica (16). Because parrotfish form bycatch in fisheries and are easily targeted by commercial and recreational spear fishermen, reserves will almost always increase the level of fish grazing within their boundaries.

Many fisheries management agencies are adopting the principle of ecosystem-based management (EBM), in which the wider functioning and requirements of whole ecosystems are considered (27). Despite the appealing premise of EBM, its implementation is generally constrained by a lack of data or appropriate analyses. How do EBM tools, such as marine reserves, influence the key processes that drive an ecosystem? This question is particularly important when considering disturbed systems, because returning one process to its “natural” level may have unexpected and even deleterious consequences for the ecosystem overall. Our results indicate that the long-term impact of Caribbean no-take marine reserves is enhanced grazing, a process that is key to the ecosystem functioning of coral reefs.

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#### Supporting Online Material

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Materials and Methods

References

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## Supporting Online Material

### Materials and methods

#### *Field sampling*

Fish species, sexual phase (for parrotfish) and length were recorded using visual fish censuses (S1), with the parrotfishes and piscivores each being consistently sampled by the same observers. Fish lengths were converted to biomass using the allometric relationships of Bohnsack and Harper (S2). Benthic composition and rugosity (vertical relief inside 1 m<sup>2</sup> quadrat) were sampled using forty 1 m<sup>2</sup> quadrats at each site in The Bahamas Archipelago. The cover of coral, macroalgae, algal turfs, encrusting coralline red algae and other substrata were quantified by randomly sub-sampling fifty 1 m<sup>2</sup> quadrats inside the reserve and both to the north and south of the reserve.

#### *Statistical methods*

Patterns of parrotfish community structure were explored using non-metric Multidimensional Scaling (MDS) of biomass data, with square root transformation. Tests for significant variation in community structure were conducted with multiple comparisons using nested ANOSIM (S3) with data from smaller spatial scales nested within larger. ANOSIM returns a statistic R, which is a measure of separation between groups where 0 indicates complete mixing and 1 represents full clustering in which all samples within groups are more similar to one another than to any sample in another group. Patterns in the total grazing of parrotfishes were analysed using nested GLM ANOVA with Box-Cox transformation and sites as random factors. Each site's mean rugosity was also added as a covariate for nested GLM so that mean biomass and rugosity were included from the level of island system to site (but not within site transects / quadrats). Correlations between rugosity and parrotfish grazing were examined using Pearson Product-Moment correlation among sites within each island system. Grazing was not correlated to rugosity in the Exuma Cays, largely because variations in rugosity were low (coefficient of variation of mean rugosity per reef was 6% for the Exuma Cays and >20% for other island systems).

#### *Effect of Nassau grouper on parrotfishes*

To investigate the feasibility of grouper consuming parrotfishes of various sizes, we established two allometric scaling relationships. Firstly, the relationship between gape width (G) and total length (TL) was established for the dominant predator, *E. striatus*, using seven anaesthetised individuals within the reserve.

Gape width,  $G = -0.5998 + (0.167 \times TL)$  with a coefficient of determination,  $r^2$ , of 0.96.

Secondly, at least three individuals of *Scarus iserti*, *Sc. vetula*, *Sparisoma viride* and *Sp. aurofrenatum* were photographed in both their terminal- (TP) and intermediate- phases (IP) to determine the relationship between fork length (FL) and maximum dorso-ventral height (H). Dimensions of the fish in each photograph were digitally analysed and the resulting scaling relationships used to estimate the maximum height of each parrotfish surveyed *in situ*.



### Grazing behaviour of parrotfishes

We adapted the statistical model of Bruggemann (*S4*) on grazing by two species of parrotfishes in Bonaire (*Sparisoma viride* and *Scarus vetula*) by extending it to multiple scarid species. The model assumes that allometric relationships between fork length and both bite rate and mouth size can be extrapolated within genera.

$$\text{Bite rate, } r, \text{ of } Sparisoma \text{ spp.} = C_{Sc} ((1088 - (17.12 \text{ FL})) - \text{Species offset}) \quad (1a)$$

$$\text{Bite rate, } r, \text{ of } Scarus \text{ spp.} = C_{Sp} ((3329 - (33.00 \text{ FL})) - \text{Species offset}) \quad (1b)$$

Bite rate,  $r$ , ( $\text{h}^{-1}$ ) is calculated as a function of species ( $s$ ), length ( $l$ ), and life phase ( $p$ ) using (1a or 1b) where FL is the fork length (cm),  $C$  is a weighting factor for life phase such that values for the genus *Scarus* ( $C_{Sc}$ ) are 0.85 for TP and 1 for IP and juveniles and those for *Sparisoma* ( $C_{Sp}$ ) are 0.80 for TP, 1 for IP and 0.84 for juveniles. Species-level offsets in the genus *Scarus* are 0 for *vetula*, 1196 for *taeniopterus*; 1714 for *iserti*. Offsets in the genus *Sparisoma* are 260 for *aurofrenatum*, 142 for *rubripinne*, 264 for *chrysopterus*, and 56 for *viride*. Offsets were based on 20 minute observations of grazing intensity in Belize ( $n=18$  per species).

Total grazing intensity, expressed as area of a reef grazed per unit time, is calculated as a function of size- and species-specific bite rates and bite sizes (*S4*).

$$\text{Bite size (allometrically scaled to length), } m, (\text{cm}^2) = M \cdot 0.001 (\text{FL}^2) \quad (2)$$

$$\text{Total grazing intensity, } TG (\text{cm}^2 \text{ h}^{-1}) = \sum_{s=1}^S \sum_{l=1}^{F_s} \sum_{p=1}^P r_{s,l,p} m_{s,l,p} \quad (3)$$

where  $S$  is the number of species,  $F_s$  is the number of size categories for species  $s$ , and  $P$  is the number of phases for species  $s$ .  $M$  is a constant that takes the value 4.013 in *Scarus* and 5.839 in *Sparisoma*.

Grazing intensity is then rescaled to the percentage of reef (2-dimensional area) grazed per hour,  $G$ , where  $ta$  is the area of a sampling unit ( $\text{m}^2$ ), which, in this case, was  $120 \text{ m}^2$ .

$$G (\% \text{ hr}^{-1}) = \left( \frac{TG}{10000} \right) \left( \frac{1}{ta} \right) \quad (4)$$

A final level of the model apportioned  $G$  into four food types (algal turfs, encrusting corallines, macroalgae and coral) but these more detailed results are not reported here.

Tests of the bite-rate portion of the model were conducted in Roatan (Honduras) and the Exuma Cays (inside and outside the reserve). Individual fish were observed for five-minute periods and their length, life phase, species and number of bites were recorded ( $n>5$  fish observations per species / life phase combination). A total of nine species / life-phase tests were carried out. In Roatan, these were *Sc. iserti* (TP and IP), *Sp. viride* (TP and IP) and *Sc. taeniopterus* (TP and IP). In the Exuma Cays, these were *Sc. iserti* (TP) inside the reserve and *Sp. aurofrenatum* (TP) inside and outside the reserve.

Predicted bite rates for *Sc. iserti* and *Sp. aurofrenatum* in the Exuma Cays were all within the 95% confidence interval of the mean for observed bite rates (in fact, with a disparity of less than 2 bites per 5 minute observation; 64.3 [obs.] versus 65 [pred.] for *Sc. iserti* and 24.6 [obs.] vs. 26.5 [pred.] for *Sp. aurofrenatum*). Note that neither of these species were used to derive the genus-specific allometric scaling relationships between FL and bite rate / bite size, making this a conservative choice of species for testing. The model predicted observed bite rates (within a 95% CI of the mean) in all but one of the six species / life phase combinations tested in Roatan. The exception was *Sp. viride* IP where the model overestimated bite rates by 36% of the upper 95% CL (predicted bite rate 50.4 five min<sup>-1</sup> vs. observed mean and upper 95% CL of 30.4 and 36.8). Bite rates of *Sp. aurofrenatum* (TP) did not differ across reserve boundaries ( $p > 0.80$ ), suggesting that differential predator abundance has little impact (if any) on the grazing rates of prey.

The extrapolation of morphometric relationships between FL and mouth size ( $m$ ) within scarid genera was not tested. However, whilst departures from this assumption are likely to influence absolute grazing rates, they are unlikely to affect our conclusions which are based on relative levels of total grazing inside and outside the reserve. Moreover, the scarid species used to generate the morphometrics are, by biomass, the most abundant representatives of each genus.

#### References

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